

Redistribution of cobalt and nickel in detached wheat shoots: effects of steam-girdling and of cobalt and nickel supply

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Abstract

Detached wheat shoots (ear with peduncle and flag leaf) were incubated for 4 d in a solution containing 1 mM RbCl and 1 mM SrCl₂ as well as 10, 40 or 160 µM NiCl₂ and CoCl₂. The phloem of some plants was interrupted by steam-girdling the stem below the ear to distinguish between xylem and phloem transport. The phloem-immobile Sr flowed mainly to the leaf lamina and to the glumes via the xylem. The Sr transport was not sensitive to steam-girdling. In contrast, the phloem-mobile Rb accumulated during the incubation time mainly in the stem and the leaf sheath. The Rb transport to the grains was impaired by steam-girdling as well as by elevated Ni and Co concentrations in the incubation solution indicating that Rb was transported via the phloem to the maturing grains and that this transport was affected by the heavy metals. Ni was removed more efficiently from the xylem in the peduncle than Co (but far less efficiently than Rb). It became evident that the two heavy metals can also be transferred from the xylem to the phloem in the stem of wheat and reach the maturing grains via the phloem.

Additional key words: phloem, rubidium, strontium, *Triticum aestivum*, xylem.

Introduction

Heavy metals are retranslocated to some extent from mature organs to young and growing tissues via the phloem (Stephan and Scholz 1993). Xylem and phloem transport both upwards in the peduncle of wheat (Kuppelwieser and Feller 1991b, Marschner 1995). Solutes may be selectively transferred from the xylem to the phloem (Feller 1989, Herren and Feller 1994, 1997a,b). The primary distribution via xylem, the retranslocation via the phloem and the transfer from the xylem to the phloem in the stem must be considered as important processes for the distribution of an element in maturing wheat shoots.

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Rubidium is easily transported in the xylem and in the phloem (Feller 1989, Kuppelwieser and Feller 1991a, Marschner 1995). Therefore it can serve as a marker for phloem-mobile solutes (Schenk and Feller 1990a). Strontium is a phloem-immobile, xylem-mobile element (Feller 1989, Schenk and Feller 1990a, Kuppelwieser and Feller 1991a, Marschner 1995). It is a rough indicator for the distribution of the xylem sap in the plant (Kuppelwieser and Feller 1991a). In detached wheat ears (with 18 cm stem) Sr is mainly translocated with the transpiration stream to the glumes while Rb can be rapidly eliminated from the xylem sap and accumulates in the lower part of the stem (Kuppelwieser and Feller 1990). In intact wheat shoots, Sr is transported to all shoot parts, especially to the glumes and the leaf lamina (organs with a high transpiration rate), whereas Rb accumulates in the stem and in the grains (Herren and Feller 1997b).

Nickel is an essential micronutrient for higher plants (Eskew *et al.* 1984, Brown *et al.* 1987, Marschner 1995, Yang *et al.* 1996a,b, 1997), but it can become toxic to plants at elevated levels (Yang *et al.* 1996b). It is mobile to some extent in the phloem and may accumulate in the grains (Kochian 1991). Plant species and cultivars differ considerably in their responses to a high Ni supply (Yang *et al.* 1996a,b).

Cobalt is essential for some plants (Marschner 1995). The Co mobility in the phloem is intermediate (Welch 1995). The distribution of Co in the plants is species-dependent (Moreno-Caselles *et al.* 1997a,b).

The phloem of wheat plants can be interrupted by steam-girdling the peduncle below the ear (Martin 1982, Feller 1989, Kuppelwieser and Feller 1990, Schenk and Feller 1990b, Fröhlich and Feller 1991). Sr fluxes are only slightly affected by steam-girdling wheat shoots below the ear but essentially no Rb passes usually through the girdled stem section (Feller 1989). Rb accumulates in the stem of girdled plants indicating that it is mainly transported via the phloem into the ear of ungirdled shoots. Phloem interruption by steam-girdling the stem below the ear of detached wheat shoots hardly affects the Sr content in the ear (Kuppelwieser and Feller 1991a,b). Steam-girdling causes an accumulation of Rb in the stem and a reduced flow of this element to the grains. Zn accumulates in grains of detached wheat shoots with an intact phloem, but not in those steam-girdled below the ear (Herren and Feller 1994). Cd is redistributed in intact field-grown wheat plants from the flag leaf lamina to the maturing grains (Herren and Feller 1997b). Furthermore, Cd can be transferred from the xylem to the phloem in the stem and reach the grains via the phloem without passing through a leaf.

Exposure of bean seedlings to excess Co, Ni or Zn inhibits the export of photoassimilates from unifoliate leaves (Samarakoon and Rauser 1979). In leaf discs of bean seedlings exposed for one day to excess Co, Ni or Zn, the loading of sucrose into the phloem is reduced (Rauser and Samarakoon 1980). This effect increases as exposure of the seedlings to the heavy metals increases up to 4 d. The absorption of Ni by the intact plant and its transfer from the roots to the shoot arc inhibited by the presence of Ni, Cu, Zn or Fe in intact soybean seedlings (Cataldo *et al.* 1978). Ni (60 μM in the nutrient medium) causes in intact wheat a strong inhibition of root growth (Taylor and Stadt 1990). Zn fed in low concentrations (0.1 - 10 μM) into the xylem of detached wheat shoots enters the ear mainly via the phloem, whereas Zn fed

in high concentrations (100 - 1000 μM) is still eliminated from the xylem sap, but loaded only in a minor percentage into the phloem (Herren and Feller 1994). Very high Zn contents may interfere in wheat with phloem transport and dry matter accumulation in the grains (Herren and Feller 1997a). It can be concluded that the phloem transport is strongly inhibited above a critical Zn level. This effect is most likely due to interferences with phloem loading or with the mass flow in the sieve tubes and not primarily by affecting phloem unloading or metabolism in the sinks.

The transport of Ni and Co via xylem and phloem in detached wheat shoots is the focus of the work presented here. The comparison with the transport of Sr (mobile in the xylem and highly immobile in the phloem) and of Rb (mobile in xylem and phloem) should allow the evaluation of the relative mobility of Ni and Co in wheat. Toxic effects on phloem transport must be considered at elevated Ni and Co concentrations.

Materials and methods

Winter wheat (*Triticum aestivum* L., cv. Arina) was grown under natural conditions in a field in Zolllikofen near Bern. Two weeks after anthesis (June 27, 1996) plants were cut with a razor blade and transported to the laboratory standing in deionized water. The plants were then recut below the flag leaf node while they were submerged in deionized water. The phloem of some plants was interrupted about 1 cm below the ear by steam-girdling according to Martin (1982).

In the culture room, each plant was incubated in a tube with 45 cm^3 feeding solution. The feeding solutions contained 1 mM RbCl and 1 mM SrCl_2 as well as equimolar concentrations of NiCl_2 and CoCl_2 in the range of 10 - 160 μM . At each concentration 4 plants with steam-girdling and 4 plants without steam-girdling were incubated for 4 d in a culture room with a 14-h photoperiod (irradiance at ear level: 120 $\mu\text{mol}(\text{photon}) \text{m}^{-2}\text{s}^{-1}$ from four Philips TL 40W/33 and two Osram Fluora fluorescent tubes), day/night temperature of 24 - 26/21 - 23 $^\circ\text{C}$ and relative humidity of 40 - 50/70 - 80 %. Evaporation was determined with four tubes (without plants) containing 1 mM RbCl and 1 mM SrCl_2 . The average evaporation was subtracted from the evapotranspiration of the incubation tubes to calculate the transpiration per plant.

The plant parts were separated after incubation and then dried at 105 $^\circ\text{C}$. The dry mass of the grains and the grain number per ear were determined. The different plant parts were heated separately in an oven at 550 $^\circ\text{C}$ for several hours. The ash was solubilized in 0.25 cm^3 1 M HCl. After mixing, deionized water (2.25 cm^3) was added. The sample solutions were diluted with 7.5 mM CsCl in 0.1 M HCl (for Rb), 36 mM LaCl_3 in 0.1 M HCl (for Sr) and 0.1 M HCl (for Ni and Co). The elements were quantified by atomic absorption spectrophotometry.

Results and discussion

In detached wheat shoots, phloem interruption by steam-girdling or increasing concentrations of Co and Ni caused no major effects on the dry mass of the grains and on the transpiration of the shoots during the incubation period of 4 d (data not shown). At the highest Co and Ni concentration used (160 μM), the transpiration tended to slightly lower values. This might be explained by toxic effects of Co and/or Ni.

Table 1. Strontium and rubidium contents [$\mu\text{g plant part}^{-1}$] in wheat shoots fed for 4 d with solutions containing Ni and Co in different concentrations (10, 40 and 160 μM). The phloem of some plants was interrupted by steam-girdling the peduncle below the ear. The feeding solution (45 $\text{cm}^3 \text{ plant}^{-1}$) contained 1 mM SrCl_2 , 1 mM RbCl and equimolar concentrations of NiCl_2 and CoCl_2 as indicated. The initial content at the beginning of the experiment was for all plant parts $<10 \mu\text{g plant part}^{-1}$. Means and standard deviations of 4 replicates are shown.

Plant part Ni + Co	Without steam-girdling			Steam-girdled below the ear		
	10 μM	40 μM	160 μM	10 μM	40 μM	160 μM
Strontium						
Grains	109 \pm 22	99 \pm 14	112 \pm 16	86 \pm 7	107 \pm 25	94 \pm 14
Glumes	482 \pm 79	684 \pm 37	827 \pm 131	424 \pm 99	809 \pm 51	938 \pm 161
Rachis	119 \pm 24	116 \pm 29	131 \pm 22	141 \pm 21	196 \pm 17	128 \pm 31
Stem	677 \pm 16	407 \pm 37	324 \pm 66	859 \pm 111	585 \pm 62	348 \pm 43
Sheath	513 \pm 77	372 \pm 24	281 \pm 97	365 \pm 51	346 \pm 66	237 \pm 52
Lamina	734 \pm 213	786 \pm 162	614 \pm 129	695 \pm 85	903 \pm 388	703 \pm 86
Rubidium						
Grains	100 \pm 29	78 \pm 18	37 \pm 18	18 \pm 25	19 \pm 18	17 \pm 13
Glumes	42 \pm 16	24 \pm 17	31 \pm 10	<10	22 \pm 23	25 \pm 23
Rachis	17 \pm 11	<10	19 \pm 13	<10	<10	28 \pm 23
Stem	688 \pm 117	661 \pm 113	1018 \pm 296	592 \pm 118	902 \pm 140	1225 \pm 350
Sheath	383 \pm 115	416 \pm 47	821 \pm 449	207 \pm 45	291 \pm 97	558 \pm 161
Lamina	76 \pm 52	106 \pm 27	163 \pm 41	67 \pm 31	178 \pm 91	201 \pm 11

Steam-girdling below the ear had no major influence on strontium accumulation in the grains of detached wheat shoots (Table 1). The highest Co and Ni concentration in the feeding solution led to a marked decrease in the Sr content of the stem, regardless of phloem intactness. This was paralleled by an increase in the Sr content of the glumes. Co and Ni may compete with Sr for cation exchange places in the xylem wall and as a consequence reduce the retention of Sr in the stem.

In contrast to Sr, the accumulation of Rb in grains of detached wheat shoots was considerably influenced by steam-girdling as well as by high concentrations of Co and Ni (Table 1). Increased Co and Ni concentrations in the feeding solution reduced the content of Rb in the grains of untreated plants to about 40 %. This is an indication for an impaired Rb transport to the grains via the phloem as a consequence of toxic concentrations of Co and/or Ni. Steam-girdling below the ear inhibited an

accumulation of Rb in the grains. Highest Rb contents were detected in the stem and high contents also in the leaf sheath. The content of the phloem-mobile Rb in the grains, glumes and rachis was considerably lower than the content of the phloem-immobile Sr, regardless of phloem intactness. Even at elevated Co and Ni concentrations, most of the Rb was retained in the stem and the leaf sheath. This results indicates that the removal of Rb from the xylem sap was not markedly inhibited by the two heavy metals at the concentrations used.

Table 2. Nickel and cobalt contents [$\mu\text{g plant part}^{-1}$] in wheat shoots fed for 4 d with solutions containing Ni and Co in different concentrations (10, 40 and 160 μM). The phloem of some plants was interrupted by steam-girdling the peduncle below the ear. The feeding solution ($45 \text{ cm}^3 \text{ plant}^{-1}$) contained 1 mM SrCl_2 , 1 mM RbCl and equimolar concentrations of NiCl_2 and CoCl_2 as indicated. The initial content at the beginning of the experiment was for all plant parts $<1 \mu\text{g plant part}^{-1}$. Means and standard deviations of 4 replicates are shown.

Plant part Ni + Co	Without steam-girdling			Steam-girdled below the ear		
	10 μM	40 μM	160 μM	10 μM	40 μM	160 μM
Nickel						
Grains	6.4 \pm 2.3	12.4 \pm 1.2	25.7 \pm 5.6	1.4 \pm 0.1	5.0 \pm 0.4	14.7 \pm 4.2
Glumes	1.4 \pm 0.2	6.1 \pm 0.9	47.0 \pm 10.5	<1	4.8 \pm 0.7	49.7 \pm 8.4
Rachis	<1	2.0 \pm 0.3	14.3 \pm 3.4	<1	1.5 \pm 0.2	14.5 \pm 2.3
Stem	9.4 \pm 1.4	28.7 \pm 2.6	77.5 \pm 21.4	12.2 \pm 0.2	46.1 \pm 5.7	112.7 \pm 16.4
Sheath	1.7 \pm 0.5	12.5 \pm 1.2	55.4 \pm 30.1	1.3 \pm 0.4	14.0 \pm 4.3	47.5 \pm 6.4
Lamina	<1	4.7 \pm 1.5	36.5 \pm 8.6	<1	5.1 \pm 3.7	45.7 \pm 9.2
Cobalt						
Grains	4.7 \pm 0.7	10.1 \pm 1.1	19.4 \pm 4.3	1.3 \pm 0.3	5.6 \pm 0.3	11.2 \pm 2.6
Glumes	1.6 \pm 0.5	7.4 \pm 0.7	54.3 \pm 11.3	1.0 \pm 0.3	7.2 \pm 1.1	63.2 \pm 13.6
Rachis	<1	2.6 \pm 0.3	16.4 \pm 3.4	<1	2.8 \pm 0.5	17.2 \pm 3.1
Stem	9.6 \pm 0.9	26.4 \pm 1.1	68.3 \pm 18.2	13.3 \pm 0.6	42.0 \pm 4.0	93.5 \pm 12.8
Sheath	2.6 \pm 0.9	14.5 \pm 1.0	52.2 \pm 27.0	2.2 \pm 0.5	15.6 \pm 4.1	43.4 \pm 6.5
Lamina	<1	8.9 \pm 2.5	43.9 \pm 10.0	<1	9.3 \pm 6.2	54.8 \pm 9.5

After steam-girdling, Ni transport to the grains is no longer possible via the phloem. Therefore, Ni was transported in such plants only via the xylem either directly to the grains or initially to the glumes and then retranslocated via the phloem to the grains. The Ni content in glumes, rachis, sheath and lamina was not markedly affected by steam-girdling (Table 2). In contrast, the Ni flux to the grains was inhibited by a phloem interruption (especially at 10 μM and to a lesser extent also at the higher Ni and Co concentrations). In untreated as well as in steam-girdled shoots, the highest Ni content was detected in the stem. At the highest heavy metal concentration applied (160 μM), the retention of Ni in stem and leaf sheath was less efficient and more Ni reached the glumes and the leaf lamina.

Compared to Ni, slightly more Co reached the glumes and the lamina indicating a less efficient removal from the xylem sap (Table 2). Furthermore, less Co than Ni accumulated in the grains. This suggests that Co was transferred less efficiently from

the xylem to the phloem and that Co has a slightly lower phloem mobility compared to Ni. Steam-girdling the peduncle below the ear led to similar effects as mentioned above for Ni.

The transport of Sr was not affected by a phloem interruption, but elevated Ni and Co concentrations decreased slightly the Sr flux via the xylem to the ear (Table 3). The Rb transport to the ear was strongly inhibited by steam-girdling at 10 μM Ni and Co. At the highest Ni and Co concentration the fluxes to the ear became very similar for steam-girdled and control plants. This overall effect was caused by a lower flux to the ear in control shoots (inhibition of phloem transport) and by an increased flux to the ear in steam-girdled shoots (less efficient removal of Rb from the xylem sap in the peduncle). At 10 μM concentration, Ni and Co reach the ear mainly via the phloem as judged from the effect of steam-girdling. However, only a minor effect of steam-girdling was detected at 40 μM concentration and essentially no effect on the transport of the two heavy metals to the ear at 160 μM concentration. Apparently the removal of these two elements from the xylem sap and their transport via the phloem to the ear was affected. As judged from similarities between the translocation of Rb, Ni and Co, it was most likely a general effect on phloem transport.

Table 3. Influence of steam-girdling below the ear on the accumulation of strontium, rubidium, nickel and cobalt in the ear and in the vegetative parts [$\mu\text{g plant part}^{-1}$] of wheat shoots fed for 4 d with solutions containing 1 mM RbCl, 1 mM SrCl₂ and equimolar concentrations of NiCl₂ and CoCl₂ (10, 40 or 160 μM). Means and standard deviations of 4 replicates are shown.

Metal	Concentration of Ni and Co [μM]	Ear		Vegetative parts	
		control	girdled	control	girdled
Strontium	10	710 \pm 117	650 \pm 97	1924 \pm 284	1918 \pm 139
	40	899 \pm 48	1111 \pm 60	1564 \pm 138	1834 \pm 406
	160	1069 \pm 130	1159 \pm 201	1219 \pm 225	1288 \pm 121
Rubidium	10	159 \pm 50	16 \pm 36	1148 \pm 232	865 \pm 141
	40	110 \pm 33	46 \pm 42	1184 \pm 108	1372 \pm 212
	160	87 \pm 47	69 \pm 58	2001 \pm 328	1984 \pm 315
Nickel	10	8 \pm 2	2 \pm 0	12 \pm 2	11 \pm 6
	40	21 \pm 2	11 \pm 1	46 \pm 5	65 \pm 13
	160	87 \pm 15	79 \pm 15	169 \pm 26	206 \pm 28
Cobalt	10	7 \pm 1	3 \pm 0	13 \pm 2	16 \pm 1
	60	20 \pm 2	16 \pm 1	50 \pm 4	67 \pm 14
	160	90 \pm 15	92 \pm 19	164 \pm 28	192 \pm 23

Conclusions

The phloem mobility is in wheat slightly better for Ni than for Co. Both elements can be removed from the xylem sap during the acropetal translocation in the peduncle. A xylem-to-phloem transfer in the stem must also be considered for Ni and Co and

may be relevant for the accumulation of these two elements in maturing grains of cereals.

Elevated concentrations of Ni and Co in the xylem may interfere in a general manner with phloem loading and transport. The transport of Rb via the phloem to the grains was strongly affected by elevated Ni and Co concentrations, although the removal of Rb from the xylem sap was only slightly influenced. In contrast, Ni and Co (introduced at concentrations of 160 μM each into the cut xylem of the detached shoots) were no more efficiently removed from the xylem sap and reached the ear with the transpiration stream. The various steps involved in the xylem-to-phloem transfer of solutes in wheat and the sensitivity of these steps to heavy metals remain to be elucidated in the future.

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